

Diel pattern of activity, mating, and flight behaviour in *Onychogomphus uncatus* (Odonata: Gomphidae)

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Key words: Odonata, dragonfly, France, irrigation canal, reproductive behaviour, flight behaviour, *Onychogomphus uncatus*.

ABSTRACT

The behaviour of *Onychogomphus uncatus*, including flight and mating activity, was studied at a fast-flowing irrigation canal. During the day, males perched in sections of the canal with a strong current and a turbulent water surface. During short flights, interactions with other con-specific and hetero-specific males occurred, particularly with *Orthetrum coerulescens*. Under conditions of high population density, the frequent occurrence and disturbances by this species often resulted in male *O. uncatus* leaving a particular section of the canal. In the late afternoon and evening, males concentrated on ground perches in the vicinity of the water. The reproductive system of *O. uncatus* was found to be 'encounter limited'. The operational sex ratio of imagines at the water was always strongly biased in favour of the males. Individual females were observed at the water during the morning and evening hours. Following pair formation there was a prolonged period of copulation away from the water. Most pair formations were observed in the morning and evening hours. They took place over water, and in the evening hours also away from the water.

INTRODUCTION

Compared with other families of Anisoptera, little is known about the activity, reproduction behaviour or habitat demands of imaginal Gomphidae. Kaiser (1974) studied the flight behaviour of male *Onychogomphus forcipatus forcipatus* (Linnaeus) at its mating sites, while Miller & Miller (1985) observed the behaviour of *O. f. unguiculatus* (Vander Linden). In the latter, a number of males often perch close together near to a potential oviposition site on a stream. They are not territorial, but take off and converge at high speed on any female that approaches the site. The female either succeeds in fleeing or is grabbed by a male. The female's rapid flight past the perched males is interpreted as a form of partner selection. Following successful pair formation, copulation is prolonged and usually takes place away from the water.

Data on the daytime activity and behaviour of imaginal *O. uncatus* (Charpentier) have been lacking up until now, apart from observations made by Schütte (1992), Rehfeldt (1995) and Suhling & Müller (1996). The observations of spatial and temporal distribution of imagines and of mating behaviour presented in this paper were made at an irrigation canal with running water in southern France, where this particular species occurred in abundance.

MATERIALS AND METHODS

Study location

Observations were conducted at the Canal des Vergières in southern France, an irrigation canal located SE of Arles on the edge of the Crau stony steppe (43°33'N, 4°51'E; cf. Rehfeldt et al. 1991; Rehfeldt 1995; Suhling 1996). The site had many structures, which were in a more-or-less natural state. It was 3-5 m wide, 0.1-0.8 m deep, and had a variable rate of flow of up to 1.2 m/s. The canal bed consisted of boulders and rocky structures with fine sand and sludge close to the canal banks. The banks themselves were in places covered with dense swamp vegetation consisting of reeds and rushes. Stony sections, less densely covered with vegetation and with rapid water current, alternated with small sections overgrown with bushes. In the winter of 1995/96 the canal was dredged and the vegetation removed, both from the water and from the banks.

Methods

From 25 June to 8 July 1996 distribution, population densities, sex ratio and perches of imagines of *Onychogomphus uncatus* were recorded close to the water, as well as at a distance of about 20 m away from the canal, especially along the path near the southern bank, for randomly chosen 25 m sections along a 300 m stretch of the canal. Sections of the canal were characterized by height of the bank vegetation and water current: strong current (> 0.8 m/s) and surface turbulence or weak current without surface turbulence.

Counts of imagines were conducted at and in the vicinity of the canal between 10:00 and 13:00 h local time (GMT + 1 h), between 13:00 and 16:00 h, and between 16:00 and 19:00 h (4 counts per 3-h period). The solar noon was at ca 11:44 h local time.

Matings were observed over the whole period of observation. I recorded how copulation wheels were formatted, the sites where mating occurred and the duration and time of day of matings.

Male flight activity and interactions with individuals of other dragonfly species were analysed with the help of video recordings (July 1996, 11:00 - 14:00 h). Eleven males were videoed for a total of 170 min. To record site fidelity, twenty males were taken in the early hours from their perches by the water, marked and kept in a cold-box before being re-released where they had been caught.

RESULTS

Distribution of imagines and ratio of the sexes

Before 13:00 h, *Onychogomphus uncatus* males occupied perches on stones close to the water (84.6%), or on low branches or stems of bank vegetation (15.4%; $n = 65$). Male population density was greatest in the morning and at midday, declining rapidly in the evening between 17:00 and 18:00 h as the water was cast into shadow from the bank vegetation (Fig. 1A). The males moved to perches without vegetation in the vicinity of the canal which had received prolonged irradiation from the sun. An un-surfaced path on the south side of the canal was particularly popular, where at this time of the day population density increased markedly. In contrast, during the day only a few individuals could be observed here.

The distribution of males along the canal was uneven, with them forming clumps of high population density (variation/mean value: 1.43; $n = 69$). This pattern of distribution suggests a preference of the males for open sections of the canal with a strong current (> 0.8 m/s) and surface turbulence. This was where the males accumulated in 1996 (76%), while in the other sections, characterized by a weaker current, only 24% of the males were to be found ($n = 69$). They often perched for considerable periods of time only a few centimetres apart on individual stones or close together on neighbouring perches (up to 7 individuals in a stretch of less than 40 cm). Males were observed to perch in sections with a weak current only when an open area offered a suitable perch (stones) directly at the water's edge. Females were observed in bushes on the edge of the canal between 11:00 and 13:00 h, and between 17:00 and 18:00 h in the evening (Fig. 1B). The sections in which they were observed always had a strong current. Only three females were observed to remain away from the water, by the unsurfaced path, during the day. Another female was observed in bushes about 200 m distant from the canal. Among adult imagines, the operational sex ratio (males:females) by the water under conditions of relatively high population density was 10:2.3 ($n = 222$).

Flight activity of males by the water

Males waited for females at the water's edge. Analyses of flight activity from video recordings consisted of taking to the air briefly (< 5 s) and of longer flights covering short distances over the water along the course of the canal. Some of the flights involved feeding. Only a few lasted for more than 10 s (Table 1). The flights

Table 1. Flight activity in *Onychogomphus uncatus* at the perching site. Recordings of 11 males for in total 170 min at noon.

Flight type	Duration:	< 5 s	5 - 10 s	> 10 s
Take-off		15	4	0
Intraspecific interactions		8	2	2
Interspecific interactions		11	3	5

usually involved interaction with other, passing or neighbouring males, or with individuals of a different dragonfly species. Males perched only a few cm apart often took off simultaneously. Conspecific males, which flew past, were usually chased over a short stretch, but without fierce attacks (16% of all flights; $n = 50$). Only one male *O. uncatus* which had been marked was recovered during the study period. It was observed to remain within a 1.5 m stretch of canal bank over a period of 190 min, perching on stones at the water's edge.

In sections with dense bank vegetation, individual males also selected plant stems – particularly dry *Juncus* stems – as perches, the height of the perches being up to 0.56 m above the water level. Here interactions with other, hetero-specific anisopterans and zygopterans were particularly numerous, particularly with the most common dragonfly, *Orthetrum coerulescens* (Fabricius), found at this location.

The flight activity of males in sections with dense vegetation was markedly greater than in sections with little vegetation (number of flights per 5 min interval: 6.25 ± 1.91 and 4.0 ± 1.84 , respectively; $U = 17.5$, $p < 0.05$, $n = 10$). Flights of *O. uncatus* males directed against individuals of *O. coerulescens* lasted for up to 17 s and involved strenuous and prolonged chases. Interactions were also observed with individuals of *Platynemesis latipes* Rambur, *Anax imperator* Leach, *Gomphus simillimus* Selys and *Libellula fulva* O.F. Müller when they happened to fly by. Disturbances through other dragonfly species resulted in *O. uncatus* males leaving their perches for ones further away (> 5 m) or at another section of the canal (26.3%; $n = 19$).

With the onset of evening (after ca 17:45 h), males left their perches by the water, which had become shaded, and settled on still illuminated areas of ground away from the canal. The short flights made from here involved taking up new perches. Intense interactions between males were not observed. Individuals would take off and return to the water, which they would overfly for a short stretch before returning to their perch away from the canal. When the area away from the water also fell into shadow the males left these perches too (after ca 18:30 h).

Pair formation and copulation

Wheel formation occurred as soon as the male had grabbed the female. Once coupled, pairs settled on large plants or bushes close to the water. Pair formation was preceded by an in-flight chase and grabbing of the female that had approached the male's perch at the water's edge. The observed copulations were distributed over the whole day, with a slight excess of activity in the morning between 10:00 and 13:00 h and in the evening between 17:00 and 19:00 h (Fig. 1C).

In 1996, four instances of wheel formation were observed in the evening hours by the path away from the water, including one as late as 19:28 h. By this time, the water of the canal had long been in shadow. The longest observed duration of complete copulation was 3 h 20 min.

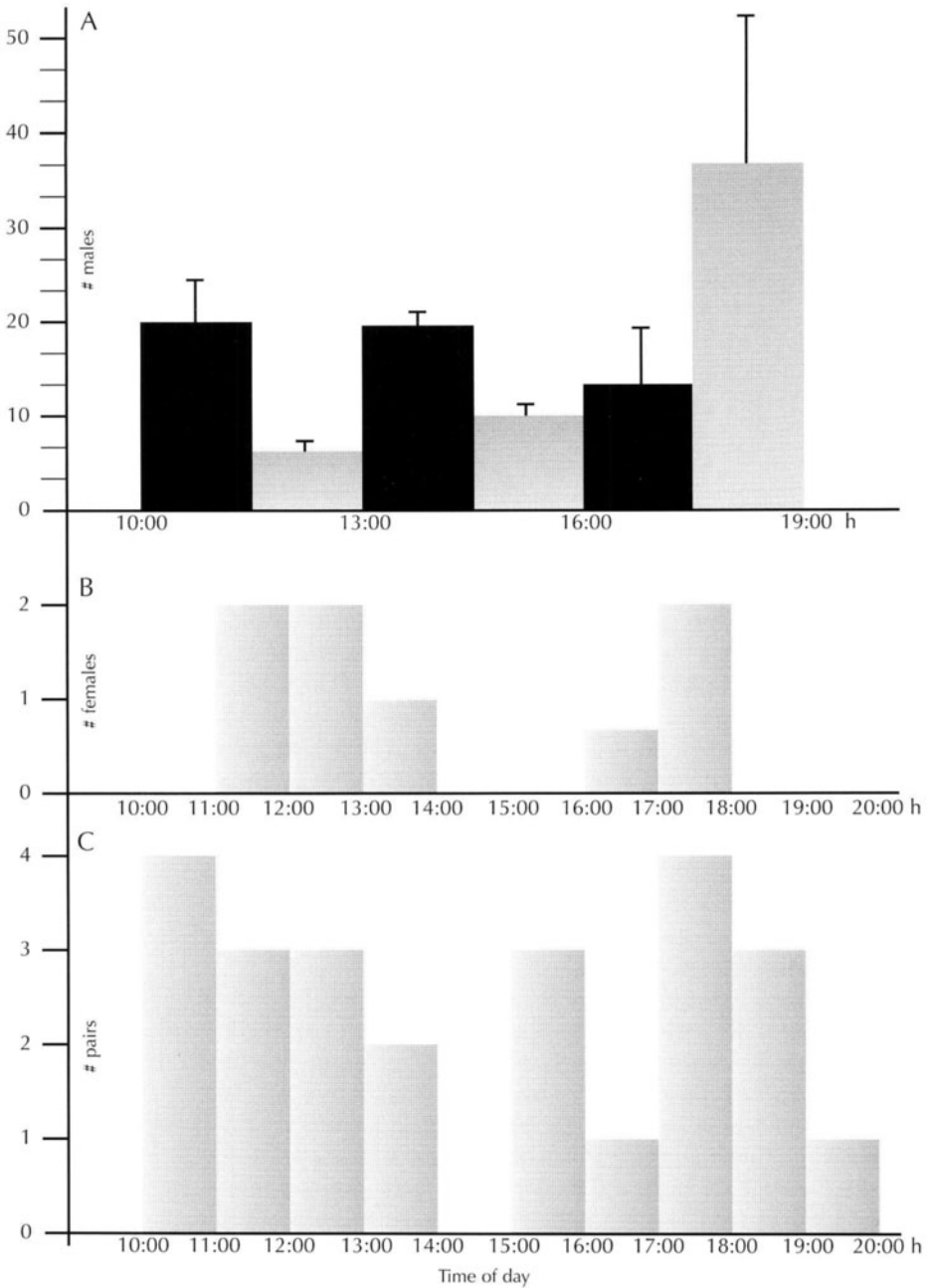


Figure 1: Activity of *Onychogomphus uncatus* at Canal de Vergière during the course of the day — number of males (A); females (B); pair formations (C). Observations were made at the water and in the surroundings from synchronous counts in June/July 1996 ($n = 6$ in each instance). Observations of males (A) are differentiated between 'water' (black) and 'surroundings' (grey)

DISCUSSION

Male *Onychogomphus uncatus* show aggressive behaviour when other individuals approach their perches or try to land close to them. Similar to *O. f. forcipatus* (Kaiser 1974) they may exhibit modest site attachment for up to 190 min. Frequent interactions with individuals of other dragonfly species – particularly with *Orthetrum coerulescens* – can, however, lead to *Onychogomphus* males giving up their perches and finding new ones on open sections of the canal bank without rival hetero-specific males. Such interactions during the course of the day may contribute to a certain degree of spatial separation in the flight activity of the various perching dragonfly species found along the course of the canal. Similar variations in the distribution of microhabitats following interspecific interactions have also been reported for the imagines of libellulid species (Rehfeldt & Hadrys 1988; Soeffing 1990).

Sex ratio at the water was strongly male biased – 10:1 in 1990/1991 (Rehfeldt 1995). The flight activity of *O. uncatus* by the water is very much a male activity, the females' behaviour at the canal being far less conspicuous; they spend most of their time perched on bushes at a greater height above the water than the males. Conrad & Pritchard (1992) refer to dragonfly reproduction systems in which oviposition sites are distributed over a wide area, so that the probability of males encountering females is fairly small, as "encounter-limited". This scheme of reproduction would apply to the behaviour of *O. uncatus*. Females make only brief flights over the water, in order to oviposit or when males chase them. The postponed ovipositions are spread over the whole day (Suhling & Müller 1996). However, mating behaviour shows clear activity maxima in the morning and evening hours, when activity is not restricted to the vicinity of the water; in the evening hours pair formation can also take place away from the canal. *Ophiogomphus cecilia* (Fourcroy) is the only other gomphid in which such behaviour has been reported (Münchberg 1932). Pairs that form in the evening hours do not oviposit on the same day, since the copulation durations in *O. uncatus* are 2.5–3.5 h (Schütte 1992).

The study of individual pair-formation strategies has proved difficult owing to the very low recovery rate of marked males. Kleemeyer (1994), for example, failed to recover a single individual from among the 266 freshly hatched *O. uncatus*, which had been marked at the study location.

Males apparently concentrate, and show highest site attachment, where the probability of encountering a female is greatest. During the day this is on sections of canal with the strongest current, while in the evening it is in illuminated areas close to the water. The high population density of males close to the water in the evening hours compared with the relatively lower population densities observed during the day suggests that, in the evening, males fly in from further afield. It is possible that factors other than the probability of encountering a female or thermoregulation play a role in causing males to leave the vicinity of the water in the evening hours. The risk of predation from web-forming spiders in the bank vegetation may also influence the distribution of male *O. uncatus* (Rehfeldt 1995). The times when adult males are most often caught in spider webs were found to

correspond closely with the temporal distribution of pair formation during the day, lying between 11:00 and 13:00 h ($n = 6$) in the morning and between 17:00 and 19:00 h ($n = 5$) in the evening. The number of males caught in spider webs in the evening hours shows that the risk for male *O. uncatus* at this time rises sharply.

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